

The University of Chicago

PHOTOPERIODIC RESPONSES  
OF GEOGRAPHICAL STRAINS OF  
*ANDROPOGON SCOPARIUS*

A DISSERTATION SUBMITTED TO THE FACULTY OF  
THE DIVISION OF THE BIOLOGICAL SCIENCES IN  
CANDIDACY FOR THE DEGREE OF DOCTOR OF  
PHILOSOPHY

DEPARTMENT OF BOTANY

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By  
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Reprinted from  
THE BOTANICAL GAZETTE  
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## PHOTOPERIODIC RESPONSES OF GEOGRAPHICAL STRAINS OF ANDROPOGON SCOPARIUS<sup>1</sup>

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 591

EUGENE C. LARSEN

### Introduction

*Andropogon scoparius* Michx. was chosen for investigation because of its extremely wide distribution and recog-

<sup>1</sup> A report of an investigation carried on at the University of Chicago at the suggestion and under the supervision of Dr. CHARLES E. OLMSTED as one in the series "Growth and development in range grasses." This work was aided in part by a grant from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago.

nized diversity (6, 7, 10, 12, 16, 22) and because of its importance as a forage grass in many parts of the United States. It has recently been used in the reseeding of abandoned, cultivated land, especially in the central prairie region (8, 9, 11, 15, 21). It is also quite well adjusted to growth in greenhouses during the hot summer months in Chicago.

Information on the photoperiodic re-

sponses of *A. scoparius* should be of value in analyzing the noticeable variations among the ecotypes when they are grown together under greenhouse or nursery conditions (10) and in understanding and explaining the reproductive and vegetative habits of the species. Such information may be of use in varietal selection and in the interpretation of growth and flowering habits of strains grown outside their native habitats. It should also be of interest to those studying the evolution and natural selection of adaptive physiological responses and their relation to plant migration.

There has been relatively little work on photoperiodic responses of various strains of native forage and range plants, although the literature in the general field of photoperiodism is extensive. The latter has recently been summarized by HAMNER (13), WHYTE (23), and BORTHWICK (5). OLMSTED (19) has referred to general literature related to photoperiodic work on grasses.

*A. scoparius* is surpassed by few species of native American plants in its wide range of habitat and distribution. It has, according to HITCHCOCK (14), been collected in all the states except Washington, Oregon, Nevada, and California. From the standpoint of abundance, its center of distribution is in the tall-grass prairie region between Texas and the Canadian line. Here it was one of the species which made up the major part of the native vegetation of the original prairie.

Its value as a forage plant varies considerably, both with season and with locality. It is generally palatable from the time it starts to grow in the spring until it begins to mature. ROGLER (20) listed *A. furcatus* as the most palatable of all the important warm-season grasses of the prairie states and stated that *A. scopari-*

*us* was its equal until around August 10, when the culms began to mature. *A. scoparius* was found to be as palatable as any grass on the range in North Dakota during the period from July 12 to 18. It does not withstand heavy spring grazing.

The range of morphological variation in this species complex has led to the recognition of several intergrading forms and varieties (12, 14, 16). HUBBARD (16) stated that the variations may be in color of the plant, length of the sessile spikelet, villousness of the sheath and leaves, compression of the sheath, or length of the hairs at the internodes of the rachis. Some of the described varieties and specific segregates have fairly well-marked geographical ranges.

Specimens of the twelve collections used in this study were sent to the National Herbarium in Washington, D.C., for identification. Dr. J. R. SWALLEN, associate curator, pointed out that strain 2 differs slightly from the others in that it has a broad, more sharply keeled lower sheath which is villous and that the staminate or pedicellate spikelets are about as large as the sessile, fertile ones. He thought that this strain is probably *A. divergens*, a species closely allied to *A. scoparius* and sometimes listed as a variety of it. He considered the eleven other collections to be *A. scoparius* and, although recognizing variation among them, did not assign varietal rank.

No cytological observations have been made upon the plants used in the present experiment. Cytotaxonomic studies (6, 7, 17) of the species and some of its named varieties have shown most of the investigated individuals to be tetraploid plants ( $2n = 40$ ), although differences in structural details of the chromosome complements are correlated with some of the observed morphological variations.

Several workers have contributed to



our recent knowledge of physiological variation exhibited by various ecotypes in grasses. NIELSEN (18), for *Panicum virgatum*, has shown what a complex of diversity one is likely to find when dealing with a large number of ecotypes from widely separated areas. OLMSTED (19), for side-oats grama, found that practically the entire range of reported photoperiodic responses was exhibited by the different ecotypes. He stated that this species cannot be classified photoperiodically except with reference to strains.

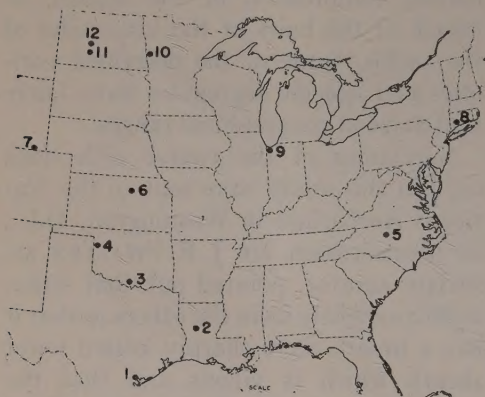


FIG. 1.—Geographical sources of strains numbered as shown.

CORNELIUS (10) has recently described the effects of source of seed of *A. scoparius* on growth, adaptation, and its use in revegetation. In his work at Manhattan, Kansas, with sixteen strains of *A. scoparius* collected from widely separated geographical areas, he reported a difference of 126 days between the first flowering dates of the northern and southern ecotypes. His northern types were earlier in maturity and lower in forage production than the southern ones. The plants originating in central latitudes were intermediate. He obtained a high seed set in the latter plants. The northern ones suffered from hot winds, and the southern ones from frost injury.

He found a highly significant correlation between the flowering date and the dry weight of a plant at the close of the season—early flowering led to low total yield. Winter injury was observed among his southern ecotypes.

The present experiment on photoperiodic responses of geographical strains of *A. scoparius* was initiated in the spring of 1946 and continued through the spring of 1947 in the greenhouses and experimental garden at the University of Chicago.

### Material and methods

Forty plants, representing twelve points of origin (fig. 1) were assembled at the University of Chicago in March and April, 1946, through the courtesy of the collectors listed in table 1, and were assigned the indicated designations. Each plant was assumed to be, and apparently was, an individual clone.

On May 1 each of the forty clones was divided, and the divisions, after being trimmed to approximately equal size, were planted in 8-inch, unglazed clay pots. Three segments of a clone were planted in each of five pots to make five identical series of forty pots each.

The pots were filled with soil consisting of a mixture of six parts of coarse sand with five parts of black loam garden soil. No fertilizer was added. This light, sandy-textured soil was used to emulate as nearly as possible the soils found in the native habitats of many of the plants.

One series (*N*) was placed on a greenhouse bench, and another (*G*), after being potted for a 10-day period, was transplanted to an experimental garden. Series *N* and *G* received Chicago natural daylength (interval between sunrise and sunset on June 21 is 15 hours and 14 minutes). The other three series were placed on movable trucks which were

wheeled into separate lightproof, ventilated sheds at 5:00 P.M. and out again at 8:00 A.M. They thus received 9 hours of natural light per day. Supplementary illumination to extend their light periods was supplied by means of three 200-watt incandescent-filament lamps mounted in individual reflectors over each of the trucks. These lights, controlled automatically, were turned on at 5:00 P.M. and were shut off at the hour necessary to provide total consecutive photoperiods of 13, 14, and 15 hours for the three series. Intensity of supplementary illumination at average foliage height

ranged from 100 to 180 foot-candles, depending on the height of a plant and its position on the truck.

Each series was so arranged that the taller plants of southern origin did not shade the smaller northern ones. As they developed, many of the taller culms were staked and tied to prevent them from falling over, breaking off, or shading surrounding plants. Pots were watered adequately to prevent temporary wilting even during hot sunny weather. Sow bugs and insect pests were controlled by the usual methods, and there were no fungus diseases of importance.

TABLE 1  
SOURCE OF TWELVE STRAINS OF ANDROPOGON SCOPARIUS

| Strain and clone    | Point of origin of clone or parental seed lot | Approximate latitude | Clone secured from                                | Sent by                                             | Accession number of agency |
|---------------------|-----------------------------------------------|----------------------|---------------------------------------------------|-----------------------------------------------------|----------------------------|
| 12A . . . . .       | Price, N.D.                                   | 47° 10'              | Northern Great Plains Field Station, Mandan, N.D. | George A. Rogler, BPI, Mandan, N.D.                 | D-139-3                    |
| 11B, C . . . . .    | Mandan, N.D.                                  | 46° 50'              | Northern Great Plains Field Station, Mandan, N.D. | George A. Rogler, BPI, Mandan, N.D.                 | D-138-3 (B)<br>D-137-4 (C) |
| 10A, B, C, D, E . . | Moorhead, Minn.                               | 47° 00'              | Field                                             | J. J. Westfall, Moorhead, Minn.                     |                            |
| 9A, B, C, D, E . .  | Dunes State Park, Ind.                        | 41° 30'              | Field                                             | E. C. Larsen                                        |                            |
| 8A, B, C, D . . . . | North Haven, Conn.                            | 41° 23'              | Field                                             | H. J. Lutz, Yale University, New Haven, Conn.       |                            |
| 7B . . . . .        | Cheyenne, Wyo.                                | 41° 05'              | Northern Great Plains Field Station, Mandan, N.D. | George A. Rogler, BPI, Mandan, N.D.                 | D-6-11                     |
| 6B, C . . . . .     | Manhattan, Kan.                               | 39° 10'              | SCS Nursery, Manhattan, Kan.                      | M. D. Atkins, SCS, Manhattan, Kan.                  | KG-1580*(B)<br>KG-480 (C)  |
| 5A, B, C, D, E . .  | Durham, N.C.                                  | 36° 00'              | Field, Duke Forest                                | H. J. Oosting, Duke University, Durham, N.C.        |                            |
| 4A, B, C, D . . . . | Arnett, Okla.                                 | 36° 10'              | Field                                             | James E. Smith, Jr., SCS, Woodward, Okla.           |                            |
| 3A . . . . .        | Ardmore, Okla.                                | 34° 10'              | SCS Nursery, Manhattan, Kan.                      | M. D. Atkins, SCS, Manhattan, Kan.                  | KG-753                     |
| 2A, B, C, D, E . .  | Alexandria, La.                               | 31° 15'              | Field                                             | J. T. Cassady, U.S. Forest Service, Alexandria, La. |                            |
| 1A, B, C, D, E . .  | Matagorda Bay, Jackson County, Texas          | 28° 15'              | SCS Nursery, Tuscon, Ariz.                        | L. P. Hamilton, SCS, Tuscon, Ariz.                  | A-2966†                    |

\* Improved selection from KG-480.

† Grown from seed from San Antonio, Texas, collection SA-4437.



Observations on culm elongation and flowering were made twice a week or oftener. Heights of the three longest tillers (to tip of outstretched leaf or inflorescence) on each plant were measured on the first and fifteenth day of each month. The three values were averaged.

On November 1, 1946, all plants were harvested by clipping just above the soil

been taken, dry weights of tops were obtained by the usual methods.

The *N* series was then placed back on the greenhouse benches, where most of the plants remained dormant during the winter months in spite of the warm temperatures. The plants in the garden (series *G*), after clipping on November 1, were left there to test their survival over



FIG. 2.—Twelve strains of *A. scoparius* grown on photoperiods of 13 hours. Left to right, below, strains 1, 2, 3, 4, 5, and 6; above, strains 7, 8, 9, 10, 11, and 12. This photoperiod was not long enough to induce internodal elongation. Southern strains show greatest leaf elongation. (Photographed September 1, 1946.)

line. Data were obtained on the total numbers of elongated and unelongated tillers. The central culm of each plant was analyzed for total length and for numbers of visible leaves, nodes, elongated internodes, and flowering branches. If inflorescences were not visible, the growing points were dissected to show whether flowers or flower primordia were present. After these measurements had

winter at Chicago. Strains 1, 2, and 5 winter-killed in the garden. All other plants survived out-of-doors.

## Results

### FLOWERING RESPONSES

The date of first flowering of a strain in any series was recorded as the date on which anthers were first exerted (first anthesis) by the first clone to flower. The



date of last flowering of a strain is defined as that on which the last-formed inflorescence in its clonal population came into anthesis. The length of flowering season of a strain was measured as the interval between these two extreme dates.

None of the twelve strains flowered on 13-hour photoperiod (table 2, fig. 2).

Plants of only strains 2, 3, 4, and 5 produced visible inflorescences on the 14-hour light period (fig. 3), although on November 1, at the time of harvest, well-developed floral primordia were present in strain 1. Strains 6–12 neither flowered nor showed elongation on 14-hour photoperiod. In the 15-hour series, strains 4 and 6–12 produced flowers (fig. 4), but

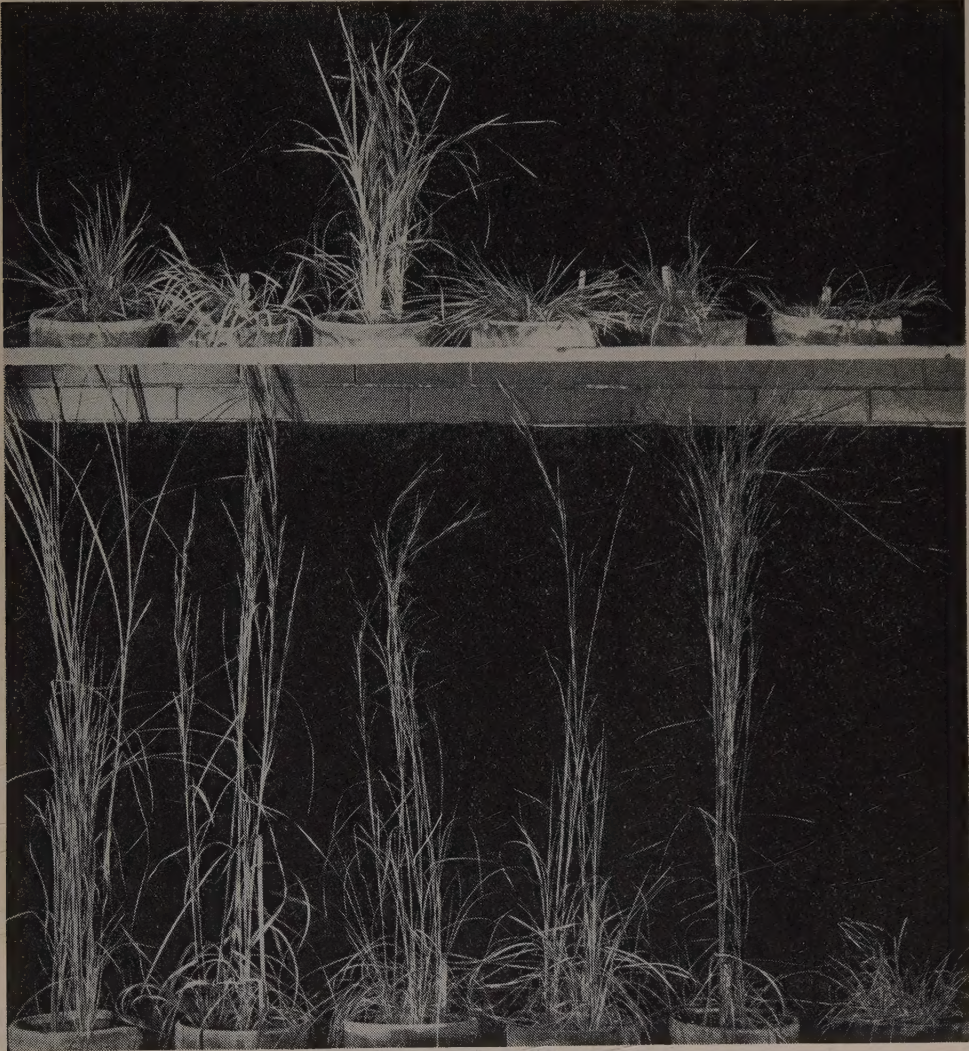


FIG. 3.—Twelve strains of *A. scoparius* grown on photoperiods of 14 hours. Left to right, below, strains 1, 2, 3, 4, 5, and 6; above, strains 7, 8, 9, 10, 11, and 12. Southern strains 1–5 showed culm elongation and flowering. Strains 6–12 remained vegetative. Strain 9 from sand dunes of Lake Michigan showed greatest vegetative growth among central and northern strains. (Photographed September 1, 1946.)



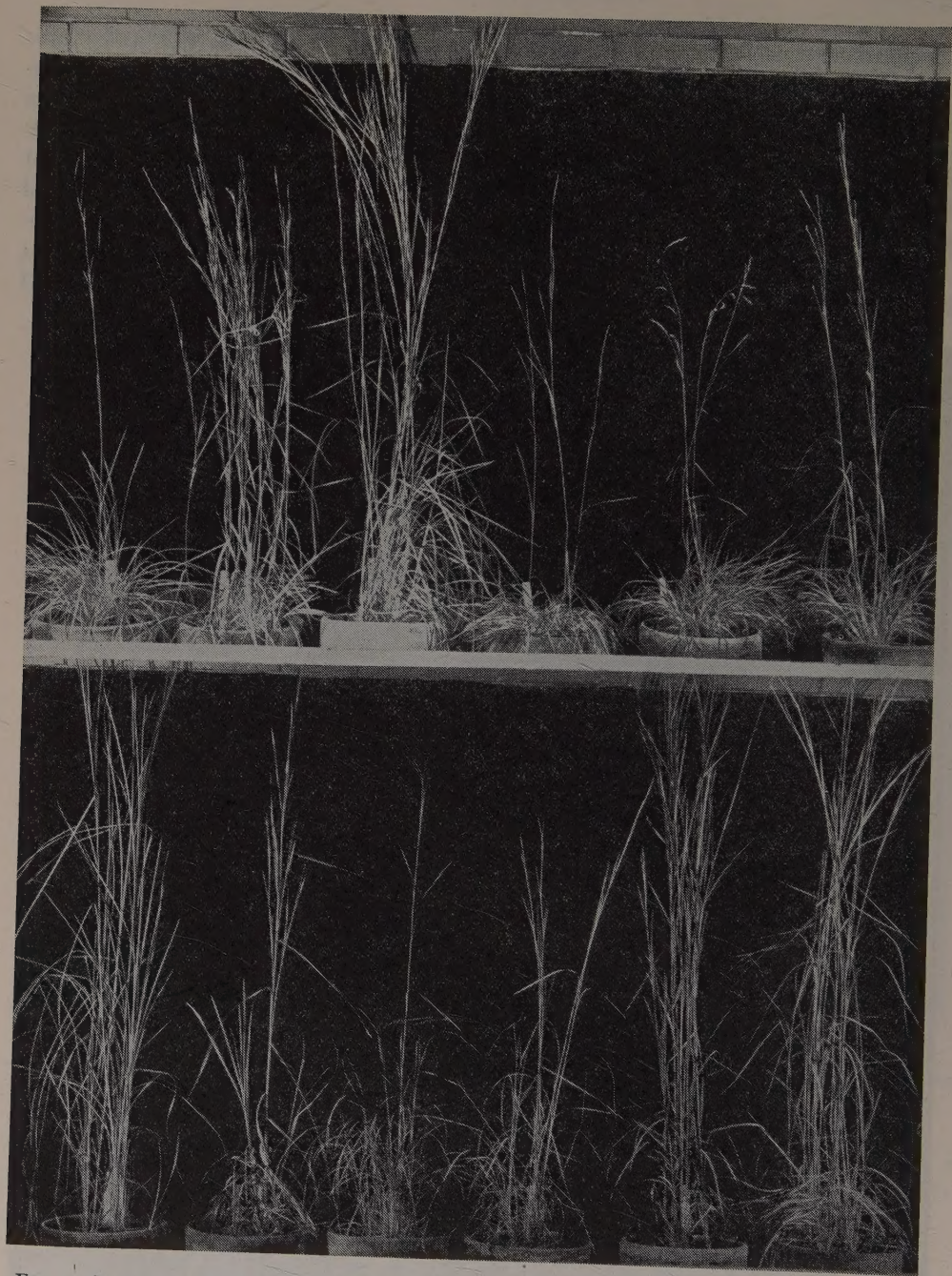


FIG. 4.—Twelve strains of *A. scoparius* grown on photoperiods of 15 hours. Left to right, below, strains 1, 2, 3, 4, 5, and 6; above, strains 7, 8, 9, 10, 11, and 12. All strains with elongated culms. Strains 1, 2, 3, and 5 did not produce flowers by time of harvesting. All plants were still green on harvesting date, November 1. (Photographed September 1, 1946.)



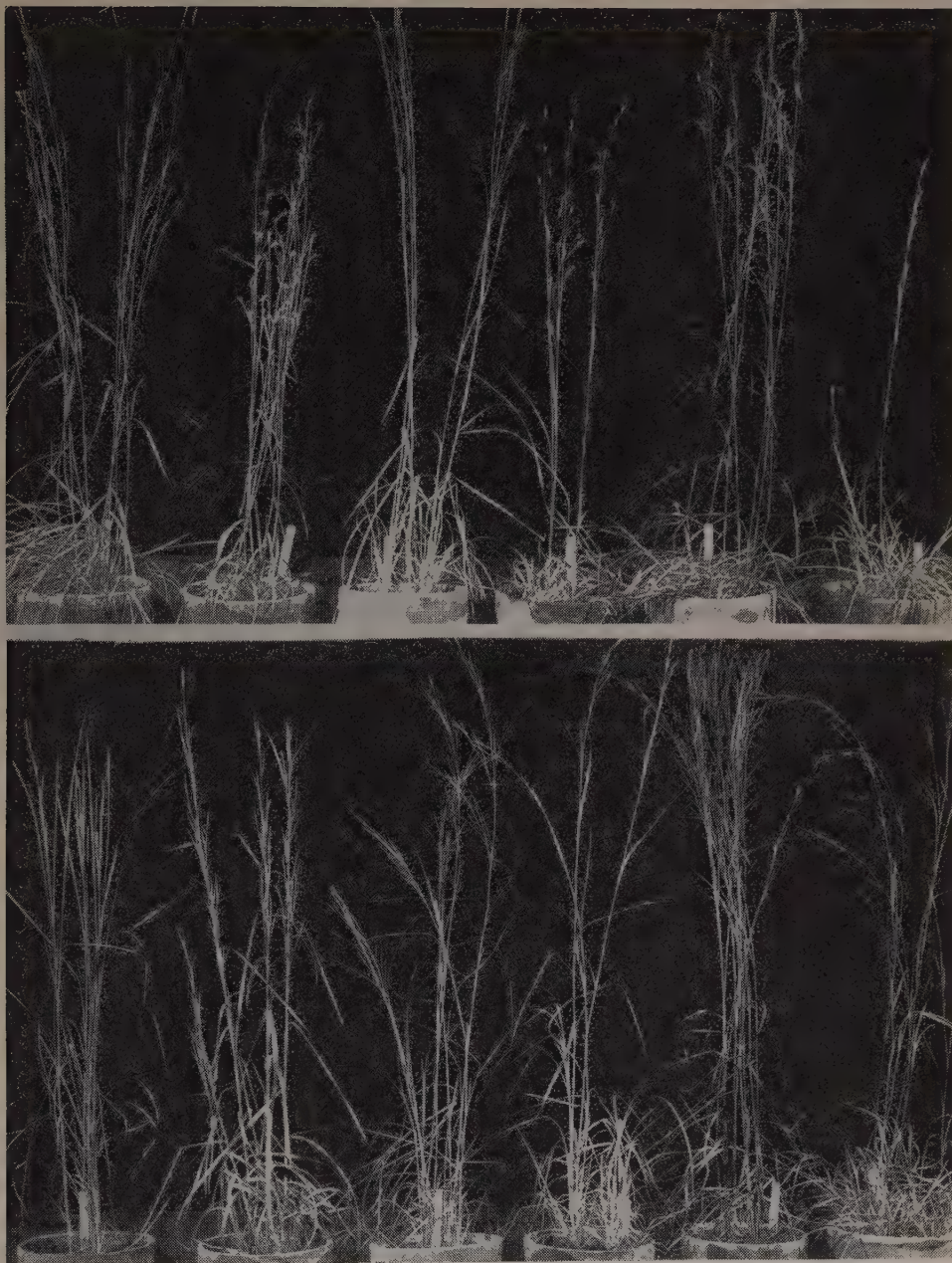


FIG 5.—Twelve strains of *A. scoparius* grown on Chicago natural daylength in the greenhouse (*N* series). Left to right, below, strains 1, 2, 3, 4, 5, and 6; above; strains 7, 8, 9, 10, 11, and 12. All strains flowered except strain 6. Northern strains have begun to enter dormancy. (Photographed September 1, 1946.)



the southern strains 1, 2, 3, and 5 had not visibly flowered at harvest time, even though culms were elongated. Dissection of their growing points showed that three of fifteen plants in strain 2, and five of ten in strain 5, had poorly developed floral primordia. Representatives of all strains flowered in the *N* series (fig. 5) except strain 6, which showed a low percentage of elongated culms. In the *G* series all clones flowered except 2*C*, 2*E*, 6*C*, and 10*D*. Plants 2*E* and 10*D* did not flower in any series.

**TIME TO FIRST FLOWERING.**—Table 2 shows the number of days after clonal division and planting on May 1 until first anthesis in each strain in each series. There was a tendency in any one treatment for southern strains to be delayed in flowering in comparison with northern ones. This tendency was most consistent in series *G*, in which all clones were most vigorous and in which most clones of all strains flowered. In this series strain 1 from Texas came into flower 65 days later than strain 12 from North Dakota.

In five out of the seven strains flowering in both the *N* and the 15-hour series, flowering was earlier on natural daylength. These data suggest a delay in the time of first flowering in these strains on the 15-hour photoperiod. This was brought out more clearly when the comparison of the two series was based on the flowering data of individual plants rather than on the earliest representatives in each strain. There was no consistent tendency for the 14-hour photoperiod either to delay or to accelerate flowering in comparison with the *N* series for the five southern strains flowering on each. In nine strains it required a longer time to first flowering in the *G* series than in the *N* series. In strain 2 the two series flowered at the same time. In strain 12 series *G* flowered first, and there was no

flowering in strain 6 in series *N*. It is possible that the delay in series *G* in comparison with *N* may have been related to the average cooler temperature conditions in the garden, which delayed early growth in series *G* and also could have lengthened the time between floral initiation and anthesis.

**FLOWERING SEASON.**—Extremes in first- and last-flowering dates of each strain and the intervals between are also shown in table 2. One is impressed with the variability among the strains in the length of flowering season in any one treatment. This showed no correlation with latitude. There was also a noticeable tendency for the flowering season of a strain on 14- or 15-hour photoperiod to be longer than in the *N* or *G* series. This was more obvious and significant when the comparison was based on individual plants rather than on those representing the extreme dates in a strain. The data suggest that in some cases the flowering season was lengthened by constant photoperiod or was shortened by the progressively decreasing daylength.

The above suggestion is borne out by the fact that, with the coming of autumn, a state of dormancy was initiated in the *N* and *G* series in which vegetative and reproductive activity ceased in all but the most southern strains, even though the autumn was very mild and frost injury to plants of series *G* was not evident until the middle of November. The plants on 13-, 14-, and 15-hour photoperiods remained green, and those in the 15-hour series continued to produce new elongated tillers. The length of the flowering seasons of some 14- and 15-hour plants was limited by harvesting.

**INTERNODAL ELONGATION.**—The time required after May 1 for evident elongation of internodes is shown in table 3. Such elongation is sometimes taken as



a criterion of the onset of reproductive activity, but, as shown later, this is not valid in *A. scoparius*. Differences between series in any one strain were probably not significant, except where elongation was completely inhibited on 13- or 14-hour photoperiods. The greatest range between strains was

in series G, in which strain 8 showed elongation in 68 days; strain 1, in 132 days. In general, it required longer for the southern strains to show elongation than the northern ones.

The length of time between first evident elongation and first flowering (table 3) was more positively correlated with

TABLE 2  
FLOWERING SEASON\*

| STRAIN NO.                        | No. OF DAYS AFTER CLONAL DIVISION ON<br>MAY 1 UNTIL FIRST FLOWERING |        |      |        | No. OF DAYS BETWEEN FIRST<br>AND LAST FLOWERING |       |       |       |
|-----------------------------------|---------------------------------------------------------------------|--------|------|--------|-------------------------------------------------|-------|-------|-------|
|                                   | Photoperiod                                                         |        |      |        | Photoperiod                                     |       |       |       |
|                                   | I4                                                                  | I5     | N    | G      | I4                                              | I5    | N     | G     |
| 12.....                           |                                                                     | 110    | 124  | 114    |                                                 | 48    | 1     | 37    |
| 11.....                           |                                                                     | 121    | 101  | 124    |                                                 | 16    | 23    | 9     |
| 10.....                           |                                                                     | 121    | 110  | 119    |                                                 | 58    | 4     | 18    |
| 9.....                            |                                                                     | 139    | 121  | 132    |                                                 | 33    | 30    | 33    |
| 8.....                            |                                                                     | 105    | 110  | 129    |                                                 | 60    | 48    | 22    |
| 7.....                            |                                                                     | 144    | 114  | 124    |                                                 | 1     | 18    | 21    |
| 6.....                            |                                                                     | 151    |      | 144    |                                                 | 28    |       | 28    |
| 5.....                            | 124                                                                 |        | 144  | 148    | 41                                              |       | 35    | 24    |
| 4.....                            | 147                                                                 | 151    | 132  | 145    | 32†                                             | 28†   | 19    | 20    |
| 3.....                            | 132                                                                 |        | 139  | 151    | 40                                              |       | 12    | 14    |
| 2.....                            | 140                                                                 |        | 144  | 144    | 32                                              |       | 14    | 28    |
| 1.....                            | †                                                                   |        | 172  | 179    | †                                               |       | 7     | †     |
| FIRST AND LAST DATES OF FLOWERING |                                                                     |        |      |        |                                                 |       |       |       |
| Photoperiod                       |                                                                     |        |      |        |                                                 |       |       |       |
| I4                                |                                                                     | I5     |      | N      |                                                 | G     |       |       |
| First                             | Last                                                                | First  | Last | First  | Last                                            | First | Last  |       |
| 12.....                           |                                                                     |        | 8-18 | 10-5   | 9-1                                             | 9-1   | 8-22  | 9-28  |
| 11.....                           |                                                                     |        | 8-29 | 9-14   | 8-9                                             | 9-1   | 9-1   | 9-9   |
| 10.....                           |                                                                     |        | 8-29 | 10-26  | 8-18                                            | 8-22  | 8-27  | 9-14  |
| 9.....                            |                                                                     |        | 9-16 | 10-19  | 8-29                                            | 9-28  | 9-9   | 10-12 |
| 8.....                            |                                                                     |        | 8-13 | 10-12  | 8-18                                            | 10-5  | 9-6   | 9-28  |
| 7.....                            |                                                                     |        | 9-21 | 9-21   | 8-22                                            | 9-9   | 9-1   | 9-21  |
| 6.....                            |                                                                     |        | 9-28 | 10-26  |                                                 |       | 9-21  | 10-19 |
| 5.....                            | 9-1                                                                 | 10-12  |      |        | 9-21                                            | 10-26 | 9-25  | 10-19 |
| 4.....                            | 9-24                                                                | 10-26† | 9-28 | 10-26† | 9-9                                             | 9-28  | 9-22  | 10-12 |
| 3.....                            | 9-9                                                                 | 10-19  |      |        | 9-16                                            | 9-28  | 9-28  | 10-12 |
| 2.....                            | 9-17                                                                | 10-19  |      |        | 9-21                                            | 10-5  | 9-21  | 10-19 |
| 1.....                            | †                                                                   |        |      |        | 10-19                                           | 10-26 | 10-26 | †     |

\* No plants flowered on 13-hour photoperiod.

† Still flowering when harvested.

‡ Floral primordia present on November 1—184 days after clonal division.

strain and treatment. Generally the southern clones required a longer interval than the northern ones in any one series. The number of days between elongation and flowering in general was greater in the 15-hour series than in the *N* series for plants flowering in each: Strain 4 shows the delay on 15 hours quite clearly. In the 14-hour and *N* series it flowered 37 days after initial elongation; in series *G*,

ably be classed as intermediate-day plants rather than short-day, since they failed to flower on 13-hour photoperiod, flowered well on 14-hour photoperiod, and failed to flower or were delayed in flowering on 15-hour photoperiod.

In summary, these data on flowering strongly suggest that (*a*) the five southern strains are intermediate-day plants in their photoperiodic responses and that

TABLE 3  
INTERNODAL ELONGATION\*

| STRAIN NO. | LENGTH OF TIME TO FIRST EVIDENT<br>ELONGATION AFTER MAY 1 |     |          |          | LENGTH OF TIME BETWEEN FIRST<br>EVIDENCE OF ELONGATION AND<br>FIRST FLOWERING |    |          |          |
|------------|-----------------------------------------------------------|-----|----------|----------|-------------------------------------------------------------------------------|----|----------|----------|
|            | Photoperiod                                               |     |          |          | Photoperiod                                                                   |    |          |          |
|            | 14                                                        | 15  | <i>N</i> | <i>G</i> | 14                                                                            | 15 | <i>N</i> | <i>G</i> |
| 12.....    |                                                           | 83  | 110      | 99       |                                                                               | 27 | 14       | 15       |
| 11.....    |                                                           | 100 | 87       | 107      |                                                                               | 21 | 14       | 17       |
| 10.....    |                                                           | 111 | 95       | 107      |                                                                               | 10 | 15       | 12       |
| 9.....     |                                                           | 90  | 95       | 99       |                                                                               | 49 | 26       | 33       |
| 8.....     |                                                           | 76  | 83       | 68       |                                                                               | 29 | 27       | 61       |
| 7.....     |                                                           | 114 | 99       | 107      |                                                                               | 30 | 15       | 17       |
| 6.....     |                                                           | 110 | 124      | 114      |                                                                               | 41 |          | 30       |
| 5.....     | 76                                                        | 76  | 76       | 99       | 48                                                                            |    | 68       | 49       |
| 4.....     | 110                                                       | 95  | 95       | 114      | 37                                                                            | 56 | 37       | 31       |
| 3.....     | 100                                                       | 114 | 95       | 114      | 32                                                                            |    | 44       | 37       |
| 2.....     | 100                                                       | 124 | 104      | 99       | 40                                                                            |    | 40       | 45       |
| 1.....     | 104                                                       | 104 | 104      | 132      | †                                                                             |    | 68       | 47       |

\* No evident internodal elongation in 13-hour series.

† Floral primordia were present 80 days after evidence of elongation.

in 31 days. On 15-hour photoperiod the interval was 56 days. Such a delay in strain 4 in the 15-hour series and the failure of strains 1, 2, 3, and 5 to flower visibly on this photoperiod suggest that these southern strains have an upper critical limit for flowering at around 15 hours or would be much delayed in flowering on photoperiods of this or greater lengths. It may be recalled that a few culms on some plants of strains 2 and 5 on 15-hour photoperiod showed floral primordia when dissected on November 1. Accordingly, strains 1-5 should prob-

(*b*) the northern strains may be long-day plants, since they are able to initiate flowers on the long natural photoperiods of June<sup>2</sup> and July in Chicago and flowered on 15-hour constant photoperiod but were inhibited from flowering on 13- and 14-hour photoperiods.

FLOWERING BRANCHES.—A flowering shoot in *A. scoparius* usually includes one or more racemes in a terminal inflorescence and four to six or more axillary flowering branches arising from the upper nodes of the culm. The average num-

<sup>2</sup> As shown by experiments carried on in 1947.



ber of such branches on the central culm at final harvest is shown in table 4. In individual cases they had been produced at nearly all the nodes of the elongated culm. In strain 5 even the axillary buds in the lower leaf sheaths often developed into flowering branches. In the other strains these lower buds usually failed to develop.

The number of axillary buds that developed into flowering branches varied with the geographical strains. In general, the southern and East Coast strains produced a greater number of such branches per culm than the northern and western ones. Strains from the extreme North and the extreme South failed to produce as many as the more centrally located strains.

There was a somewhat direct relationship between the height and number of nodes of a culm and the number of flowering branches. The plants in the garden produced more flowering branches than those on any other treatment. In six of the seven strains which flowered in both the *N* and the 15-hour series, those plants on 15-hour photoperiod produced fewer flowering branches than those in the *N* series.

#### VEGETATIVE RESPONSES

**TILLER NUMBER AND ELONGATION.**—The most striking effect of photoperiodic treatment was upon the degree of elongation of leaf blades and sheaths and internodes of stems. There apparently is a distinct critical photoperiod above which plants of a strain showed marked elongation of culms and leaves and below which such elongation was exceedingly limited. None of the plants on 13-hour photoperiod showed such elongation; all of them on 15-hour photoperiod did so (table 5, figs. 2-4). The critical photoperiod for elongation in the species is ap-

parently between 13 and 15 hours. On 14-hour photoperiod, plants of the southern strains (1-5) elongated and produced flowers, while those of northern strains (6-12) showed no elongation. Strain 5 originated at latitude 36° N., strain 6 at 39° N.

The plants on 13-hour photoperiod were much like those on other treatments in growth habits for a few weeks after planting. Their rate of height growth

TABLE 4  
AVERAGE NUMBER OF FLOWERING BRANCHES  
PER CENTRAL CULM\*

| STRAIN<br>NO. | PHOTOPERIOD |    |          |          |
|---------------|-------------|----|----------|----------|
|               | 14          | 15 | <i>N</i> | <i>G</i> |
| 12.....       |             | 3  | 4        | 6        |
| 11.....       |             | 5  | 6        | 5        |
| 10.....       |             | 2  | 5        | 5        |
| 9.....        |             | 5  | 4        | 8        |
| 8.....        |             | 7  | 8        | 11       |
| 7.....        |             | 2  | 5        | 4        |
| 6.....        |             | 6  |          | 9        |
| 5.....        | 10          |    | 12       | 13       |
| 4.....        | 5           | 6  | 6        | 6        |
| 3.....        | 8           |    | 8        | 14       |
| 2.....        | 7           |    | 7        | 14       |
| 1.....        |             |    | 5        | 7        |

\* Based on flowering plants only.

then diminished rapidly, and they showed little increase in height through the remainder of the season. The southern strains grew more rapidly than the northern ones at first and continued to grow for several weeks after the northern ones appeared static. The latter showed little increase in height after the first 2-4 weeks on 13-hour photoperiod, even though new leaves continued to form. However, the blades and sheaths and internodes failed to elongate normally. Large buds formed in the axils of the leaf sheaths. The expansion of these buds forced the leaf sheaths open, spreading the two-ranked leaves apart. Some of the

fanlike rosettes approached a horizontal plane, but more of them oriented themselves at right angles to the rays of the sun (fig. 6).

Individual plants which failed to show elongation all produced large numbers of tillers. Apparently conditions which hinder elongation or floral initiation may favor an increase in total tiller number. In general, the plants which did not

from each plant, and the total number of leaves on it was recorded (table 6). In some strains there was no obvious correlation between number and photoperiod or the amount of culm elongation. In part this may have resulted from the difficulties in making accurate counts of the leaves on the unelongated culms in the 13- and 14-hour series. Strains 7, 9, and 10, in which these difficulties were

TABLE 5  
TILLER NUMBER

| STRAIN NO. | AVERAGE NO. OF TILLERS PER PLANT<br>ON NOVEMBER 1 |    |    |    |    | PERCENTAGE OF TOTAL NO. OF TILLERS<br>THAT ELONGATED* |    |    |    |
|------------|---------------------------------------------------|----|----|----|----|-------------------------------------------------------|----|----|----|
|            | Photoperiod                                       |    |    |    |    | Photoperiod                                           |    |    |    |
|            | 13                                                | 14 | 15 | N  | G  | 14                                                    | 15 | N  | G  |
| 12.....    | 24                                                | 11 | 17 | 9  | 40 | .....                                                 | 35 | 26 | 29 |
| 11.....    | 11                                                | 18 | 21 | 12 | 33 | .....                                                 | 20 | 50 | 11 |
| 10.....    | 7                                                 | 10 | 10 | 8  | 31 | .....                                                 | 27 | 16 | 9  |
| 9.....     | 9†                                                | 9† | 9  | 6  | 39 | .....                                                 | 59 | 44 | 45 |
| 8.....     | 18                                                | 14 | 11 | 13 | 14 | .....                                                 | 39 | 22 | 51 |
| 7.....     | 7†                                                | 9† | 11 | 15 | 38 | .....                                                 | 35 | 63 | 17 |
| 6.....     | 27                                                | 25 | 12 | 32 | 93 | .....                                                 | 66 | 8† | 27 |
| 5.....     | 21                                                | 11 | 7  | 11 | 14 | .....                                                 | 26 | 53 | 27 |
| 4.....     | 21                                                | 17 | 9  | 19 | 38 | .....                                                 | 30 | 58 | 24 |
| 3.....     | 26                                                | 12 | 9  | 16 | 24 | .....                                                 | 27 | 40 | 28 |
| 2.....     | 10                                                | 7  | 5  | 14 | 13 | .....                                                 | 43 | 33 | 16 |
| 1.....     | 9                                                 | 7  | 7  | 8  | 27 | .....                                                 | 42 | 44 | 26 |

\* No elongation on 13-hour photoperiod.

† Large buds not counted as tillers.

‡ Plant did not flower.

flower produced more tillers than those that did. The 15-hour plants, when taken as a whole, produced the smallest number of tillers of all the treatments.

At final harvest, ten of the strains showed a higher percentage of tillers elongated on 15-hour photoperiod than in the N series. The excepted strains are strain 7, in which insect injury to plants on 15-hour photoperiod probably retarded elongation, and strain 11, one clone of which did not flower in this series.

NUMBER OF LEAVES.—At the time of harvest, the central culm was removed

not great, definitely had more leaves per culm under the 13-hour treatment, with no elongation, than in the other series. In contrast, in the southern strains 1, 2, 3, and 4, the numbers were lower in the plants on 13-hour treatment in which no elongation occurred than in the same clones in the other series. These southern strains, however, were much taller in the 13-hour series than were the other strains which produced more leaves per central culm. In the other series, in general, the southern strains produced more leaves per culm than the northern ones. Strain



5 from North Carolina averaged twenty-one leaves on each central culm in series *N*.

**GROWTH IN HEIGHT.**—Height measurements taken periodically through the summer of 1946 showed that, on 13-hour photoperiod, strains 1-4 reached their maximum height before July 1. On 14-hour photoperiod, strains 1-2 grew in height until October 15; strains 3-5 continued to increase until about September 15 to October 1, while strains 6-12 showed little change in height after July 1. In the other series in the plants which flowered, growth curves tended to begin to level off just prior to first anthesis, and most of these plants reached their maximum height at about the time of full anthesis.

At harvest time the central culm from each pot was clipped at ground level and was measured from the cut end to the tip of the outstretched leaf or inflorescence. The averaged values are given in table 6. The flowering plants were taller than the nonflowering. The shortest plants were in the northern strains 5-12 on 13-hour

photoperiod. Southern strains 1-4 in this series were taller, even though they failed to show marked internodal elongation or to flower. On 14-hour photoperiod, strains 1-5 were very tall, but strains 6-12 were about the same height as on 13-hour photoperiod (figs. 2, 3). In general, all strains were much taller in the 15-hour, *N*, and *G* series than on 13-hour



FIG. 6.—Strain 12 from North Dakota; characteristic rosette condition developed in northern strains grown on 13-hour photoperiod. Leaves continued to form even though blades, sheaths, and culms failed to elongate normally. (Photographed September 29, 1946.)

TABLE 6  
CENTRAL CULMS; DATA OF NOVEMBER 1

| STRAIN<br>NO. | AVERAGE NO. OF VISIBLE LEAVES |      |      |          |          | AVERAGE MAXIMUM HEIGHT (CM.) |     |     |          |          |
|---------------|-------------------------------|------|------|----------|----------|------------------------------|-----|-----|----------|----------|
|               | Photoperiod                   |      |      |          |          | Photoperiod                  |     |     |          |          |
|               | 13                            | 14   | 15   | <i>N</i> | <i>G</i> | 13                           | 14  | 15  | <i>N</i> | <i>G</i> |
| 12.....       | 8.5                           | 11.1 | 8.5  | 9.7      | 8.0      | 18                           | 15  | 103 | 58       | 78       |
| 11.....       | 8.8                           | 8.0  | 10.4 | 11.2     | 7.5      | 21                           | 24  | 52  | 109      | 68       |
| 10.....       | 11.5                          | 9.3  | 10.3 | 7.3      | 4.9      | 18                           | 22  | 47  | 47       | 44       |
| 9.....        | 17.3                          | 12.4 | 11.6 | 11.3     | 11.9     | 36                           | 49  | 93  | 77       | 95       |
| 8.....        | 12.0                          | 9.3  | 11.6 | 12.0     | 13.0     | 23                           | 32  | 70  | 77       | 95       |
| 7.....        | 18.7                          | 9.0  | 9.7  | 10.0     | 7.3      | 18                           | 31  | 90  | 108      | 60       |
| 6.....        | 8.7                           | 7.3  | 13.2 | 7.5      | 11.0     | 39                           | 30  | 107 | 43†      | 69       |
| 5.....        | 11.2                          | 13.2 | 18.3 | 21.3     | 17.3     | 26                           | 107 | 100 | 121      | 98       |
| 4.....        | 7.3                           | 11.5 | 13.0 | 13.1     | 10.2     | 49                           | 69  | 97  | 112      | 55       |
| 3.....        | 8.0                           | 12.8 | 10.3 | 15.5     | 17.0     | 63                           | 100 | 53* | 108      | 95       |
| 2.....        | 8.3                           | 15.4 | 15.9 | 13.3     | 16.4     | 55                           | 106 | 86  | 103      | 77       |
| 1.....        | 8.0                           | 15.8 | 11.8 | 13.8     | 14.3     | 82                           | 119 | 110 | 99       | 89       |

\* Plant weak.

† Plants failed to flower.

photoperiod. The various clones of a strain and series in the greenhouse were more variable in height than in the garden.

**TOP WEIGHT.**—At harvest time the tops were clipped just above soil level, and oven-dry weights were determined (table 7). In all strains except 7 and 11, plants of series G yielded more than the comparable plants in any of the other four series. This probably was related in

however, produced more dry weight than any of the others in series G and stood in second or third rank in the 13-, 14-, and 15-hour series. Apparently this strain, native to open sterile dune sand, is able to respond vigorously to improved soil and water relations.

In many strains the effect of photoperiod upon dry weight was striking. Strains 1 and 2 yielded more in the 14-hour series than in the 13-hour, 15-hour, or *N* series. Many of the northern strains produced only about half as much weight on 13-hour photoperiod as they did on 15 hours. They are usually dormant under natural conditions when day-lengths are 13 hours or lower. Some of them also yielded more on the 15-hour treatment than in the corresponding *N* series. This may be correlated with the effect of the former in inducing continued vegetative and reproductive activity, while the plants in the *N* series became relatively dormant after flowering on the decreasing natural daylength.

It should be emphasized that the differences in dry-weight yield among the 13-, 14-, and 15-hour series are an expression of photoperiodic effects and cannot be related to the differences in total irradiation as affecting opportunity for photosynthesis and carbohydrate accumulation. The three series were all exposed equally to 9 hours of natural light per day and differed only in their lengths of exposure (4, 5, or 6 hours) to supplementary illumination of an intensity too low to be very effective in carbohydrate synthesis.

### Discussion

The results have shown that *A. scoparius* as a species is strikingly sensitive to photoperiod. It has also demonstrated conclusively that there is considerable differentiation within this widely

TABLE 7

AVERAGE DRY WEIGHT (GM.) PER PLANT OF  
CLIPPED TOPS, NOVEMBER 1, 1946

| STRAIN<br>NO. | PHOTOPERIOD |      |       |          |          |
|---------------|-------------|------|-------|----------|----------|
|               | 13          | 14   | 15    | <i>N</i> | <i>G</i> |
| 12.....       | 24.7        | 23.5 | 49.0  | 18.5*    | 113.0    |
| 11.....       | 18.0        | 20.0 | 45.9  | 59.1     | 52.3     |
| 10.....       | 12.9        | 17.1 | 24.8  | 20.5     | 37.0     |
| 9.....        | 53.7        | 57.7 | 81.8  | 61.0     | 344.8    |
| 8.....        | 21.9        | 26.2 | 45.0  | 35.6     | 92.0     |
| 7.....        | 5.0         | 39.7 | 36.0  | 96.7     | 83.0     |
| 6.....        | 53.0        | 22.0 | 117.4 | 56.2     | 231.7    |
| 5.....        | 29.5        | 57.7 | 64.6  | 73.5     | 123.7    |
| 4.....        | 43.5        | 52.1 | 57.8  | 81.4     | 91.2     |
| 3.....        | 62.2        | 47.0 | 29.5* | 80.2     | 180.0    |
| 2.....        | 52.5        | 78.9 | 51.3  | 67.0     | 253.4    |
| 1.....        | 55.6        | 89.2 | 79.7  | 55.3     | 327.8    |

\* Plants weak.

large part to the limiting effect of reduced light intensity in the greenhouse upon the four series grown indoors as well as to the effect of pot culture. The degree of this limitation was most striking in strain 9 from the Indiana sand dunes. However, differences in yield among strains and in relation to photoperiodic treatment were obvious in the greenhouse plants. The southern strains, in general, yielded more than the northern ones in all series. The southern plants are more robust and grow vegetatively for a longer time. In their native habitats they have a longer frost-free period. Strain 9 from Indiana Dunes State Park,



ranging species as to the nature of the photoperiodic response. Somewhat similar differentiation in side-oats grama has previously been reported by OLMSTED (19).

The data for 1946 show that culm elongation, dry-weight yield, and floral initiation are sharply controlled by the photoperiod upon which the plants are grown. There is a critical lower photoperiod below which dry-weight yield is low, culms do not elongate, and floral initiation is lacking. For strains of latitude  $36^{\circ}$  and southward, this critical photoperiod lies between 13 and 14 hours; for strains of latitude  $37^{\circ}$  and northward, between 14 and 15 hours. Above this critical photoperiod, all strains showed culm elongation and relatively vigorous vegetative growth. Additional experiments in 1947 indicated that in many strains an 18-hour photoperiod tended to induce earlier culm elongation than did a 15-hour one or than did natural daylength at Chicago.

All these data suggest a long-day status of the species. That this is not true of all the strains, however, is shown by the fact that strains 1, 2, 3, and 5 either failed to flower or were much delayed in flowering on 15-hour photoperiod in comparison with a 14-hour one. For floral initiation and vigorous and rapid flowering, they seem to require a narrow range of photoperiods lying between 13 and 15 hours. They would thus be classed as intermediate-day plants. Similar findings were made by ALLARD (1), by ALLARD and EVANS (2), and by ALLARD and GARNER (3) in related species or genera. CORNELIUS (10) found in his collection of strains of *A. scoparius* grown at Manhattan, Kansas, that the southern ones were delayed in flowering until the short days of autumn and were likely to be injured by frost while still vigorously grow-

ing. In their native latitudes they experience photoperiods favorable to floral initiation early enough to have flowered and entered dormancy before any danger of frost but in Kansas were not exposed to such photoperiods until August or later.

An intermediate-day status for the northern strains (6-12), based on flowering responses, has not been conclusively demonstrated, and they may probably be classed as long-day plants with a critical photoperiod between 14 and 15 hours. One clone each of strains 6-12 flowered on 18-hour photoperiod in 1947 but were somewhat delayed in doing so in comparison with the same clonal divisions on natural daylength or on 15-hour photoperiod. It is very likely that the northern strains flower normally over a wider range of photoperiods than do the southern ones. The time of onset of flowering in them, in July or August, in their native habitats suggests that these northern strains initiate flowers during the season of long natural photoperiods in June and July. The experimental data indicate in part that possibly the natural decreasing photoperiods are more favorable for the later development of inflorescences than are constant long ones. The experimental results also lead one to the conclusion that the decrease in natural daylength below a certain level may be partially responsible for the cessation of vegetative and reproductive activity and the onset of dormancy, especially in the northern strains.

Since the great majority of species of *Andropogon* are tropical or subtropical in distribution, it is very likely that *A. scoparius* originated in low latitudes in which an intermediate- or short-day response would be typical. It is likely that the northward migration of the species into the higher latitudes of the United

States took place along at least two routes: through the central grassland region and up the Atlantic coastal plain.

On the basis of morphological similarities and dissimilarities, it seemed possible to separate the twelve strains used into three groups: northern (strains 7, 10, 11, 12), central (strains 3, 4, 6, 9), and southern or eastern (strains 1, 2, 5, 8). It will be noted by referring to figure 1 that these morphologically differentiated groups are not correlated solely with latitude but with altitude, physiographic provinces, and vegetational regions also, and, for the central and eastern and southern groups, with the suggested routes of migration. It is possible that the groups are genetically differentiated from one another by reason of isolation of environment. Within each group there may have been a greater chance for genetic interchange than between groups. If this hypothesis is correct, it is interesting that two of the three groups include both intermediate- and long-day strains, suggesting the evolution of the long-day response along both of the suggested routes of migration northward. Since the species is a warm-season grass in accord with its probable origin in low latitudes, a northward migration would have been dependent upon the evolution of the long-day or day-neutral habit in the migrating populations, or at least upon an increase in length of the upper critical photoperiod above that now found in strains 1, 2, 3, and 5. Only in this way could the species have become adjusted to flower during the short growing seasons of the northern latitudes while still retaining the high minimum-temperature requirements for growth still characteristic of it.

### Summary

1. Forty plants of *Andropogon scoparius* from twelve points of origin were assembled at the University of Chicago

greenhouses in the spring of 1946 and were numbered as shown in figure 1. The twelve geographical strains represented a latitudinal range of approximately  $21^{\circ}$  from Jackson County, Texas, to Price, North Dakota, and an east-west range from North Haven, Connecticut, to Cheyenne, Wyoming. Their responses to natural daylengths in greenhouse and garden and to constant photoperiods of 13, 14, and 15 hours in the greenhouse were investigated.

2. Growth and development were found to be sharply sensitive to length of photoperiod. None of the twelve strains flowered on 13-hour photoperiod. Plants of only southern strains 2, 3, 4, and 5 produced visible inflorescences on the 14-hour light period. Strain 1 had initiated floral primordia in this series when harvested on November 1. In the 15-hour series, strains 4 and 6-12 produced flowers, but the southern strains 1, 2, 3, and 5 had not visibly flowered at harvest time, even though culms were elongated. Representatives of nearly all the strains produced visible flowers on natural daylength, the southern ones later than the northern. Strains 1-5 should probably be classed as intermediate-day plants rather than short-day, since they failed to flower on 13-hour photoperiod and also failed to flower or were delayed in flowering on 15-hour photoperiod. The northern strains may be long-day plants, since they are able to initiate flowers on long photoperiods but were inhibited from flowering on 13- and 14-hour photoperiods.

3. There apparently is a distinct critical photoperiod above which plants of a strain showed marked elongation of culms and leaves and increase in dry weight and below which such elongation or increase was exceedingly or somewhat limited. None of the plants on 13-hour photoperiod showed elongation; all of



them on 15-hour photoperiod did so. On 14-hour photoperiod, plants of the southern strains (1-5) elongated and produced flowers, while those of northern strains (6-12) showed no elongation. Strain 5 originated at latitude 36° N., strain 6 at 39° N.

4. With the coming of autumn a state of dormancy was initiated in the two series on natural daylength; vegetative and reproductive activity ceased in all but the most southern strains. Plants on 13-, 14-, and 15-hour photoperiods remained green, and those in the 15-hour series continued to produce new elongat-

ed tillers. At final harvest, in general, the strains showed a higher percentage of tillers elongated on 15-hour photoperiod than in the indoor series on natural day-length.

The assistance of those who supplied the clonal material and the help of Dr. CHARLES E. OLMSTED in carrying out this experiment are gratefully acknowledged.

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